BREEDING BIOLOGY OF THE BLACK TIT (*PETROICA MACROCEPHALA DANNEFAERDI*) ON THE SNARES ISLANDS, NEW ZEALAND

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ABSTRACT

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Black tits (*Petroica macrocephala dannefaerdi*) bred at a density of 2.7 pairs/ha in *Olearia/Brachyglottis* forest on the Snares Islands. The total population was conservatively estimated at 500 pairs in November 1987. Characteristics of 49 nest sites are documented. All sites were well protected from above, but would have been very accessible to a predatory mammal. Clutch size was three (n = 25) or two (n = 5). Laying occurred between 21 October and 2 December in 1987, peaking in the first week of November. Each pair raised a single brood of about 2.5 chicks.

Productivity of black tits was much lower than for populations of New Zealand tits (*P. macrocephala*) at lower densities. We suggest that the high density of black tits is due to the absence of predatory mammals on the Snares Islands, and low per pair production of young is due to high intra-specific competition, leading to a reallocation of resources and the production of fewer, more competitive offspring.

KEYWORDS: black tit - *Petroica macrocephala* - Snares Islands - breeding - density effects - island effects.

INTRODUCTION

Landbirds breeding on islands typically occur at higher densities, have lower productivity, and invest more in each offspring raised, than conspecific mainland populations (Cody 1966, Stamps & Buechner 1985). This tendency towards K-selection in island birds has been attributed to the effects of high intra-specific competition for a limiting resource, usually either food or breeding space (Stamps & Buechner 1985 and references therein).

New Zealand tits (*Petroica macrocephala*) are small sedentary flycatchers that are widely distributed in scrub and forest throughout New Zealand. They occur on the North Island and offshore islands (pied tit *P. m. toitoi*), South Island, Stewart Island and offshore islands (yellow-breasted tit *P. m. macrocephala*), Chatham Islands (Chatham Island tit *P. m. chathamensis*), Snares Islands (black tit *P. m. dannefaerdi*) and Auckland Islands (Auckland Island tit *P. m. marrineri*). New Zealand tits breed from August to February, building nests in semi-enclosed locations (e.g. tops of stumps, crevices in trees and banks, dense vegetation; Wilkinson & Wilkinson 1952, Oliver 1955, Soper 1976). Two to five eggs are laid on consecutive days, with two or three broods raised per season (Gibb 1961, Kearton 1979).

The black tit (Fig. 1) is the only melanistic form of *P. macrocephala*, and is confined to the relatively unmodified Snares Island Nature Reserve (48°02′ S, 166°36′ E). Although both sexes are dark, females are slightly browner than males, and can also be distinguished from males by behaviour (Fleming 1950a,b, Best 1975). As in other populations of *P. macrocephala*, females rarely sing, do all the incubation and brooding at the nest, and are fed by males during incubation (Fleming 1950a,b). On the Snares Islands there are no predators which specialise on small forest birds or their nests, and so the population is likely to be controlled by food supply. In contrast, mainland populations of pied and yellow-breasted tits are preyed upon by a suite of native

Figure 1. (Top) Male black tit carrying food to nest.

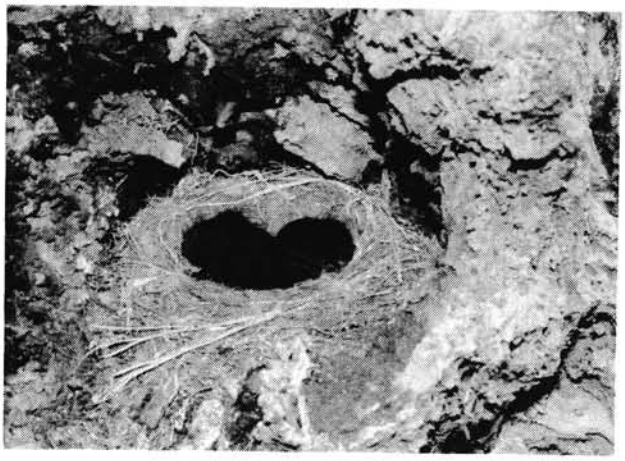

Figure 2. (Bottom) Black tit nest containing three chicks, age about 16 days.

and introduced predators (see e.g. King 1984). However, birds breeding on the Snares Islands have to contend with an unusual form of nest destruction. An estimated 2.75 million pairs of sooty shearwaters (*Puffinus griseus*) breed on the Snares Islands at a mean density of 11,600 pairs/ha under *Olearia* forest (Warham & Wilson 1982). Each evening from September to April, many thousands of shearwaters, along with lesser numbers of common diving petrels (*Pelecanoides urinatrix*), crash through the canopy to land near nesting burrows. Any tit nest that is not adequately protected from above would be vulnerable to inadvertent damage by these petrels (see also Best 1975).

We document details of nesting density, population size, nest site, clutch size and timing of breeding for black tits during the 1987 breeding season. Comparisons are made with other tit populations to investigate whether the breeding system of *P. macrocephala* varies at different breeding densities.

MATERIALS AND METHODS

Black tits were studied in *Olearia lyalli* and *Brachyglottis stewartiae* forest on the Snares Islands between 7 November and 8 December 1987. Observations were also made during longer visits by C. M. Miskelly over the previous five summers. Nests of virtually all pairs breeding within 250 m of the research station on

Station Point were located. Twenty birds had been colour-banded in the 1986-87 season, and nests were located for all 10 known surviving banded adults in late 1987, suggesting that few nests or mated pairs were missed.

Most nests were found by listening for begging calls of the female when she came off the nest. A few were found by checking likely nest sites, or sites known to have been used in other years. Females were followed to nests with little difficulty, and both sexes were tolerant of our presence near the nest. Nests were checked only when females were absent; we did not disturb birds from the nest.

Nest site characteristics were recorded for 37 nests used in November 1987, plus 12 sites known from previous years. We recorded details of the surrounding forest, and specific details of the site (see Results). Canopy cover was assessed as the percent of the area of a 10 m radius above the nest which was obscured by vegetation. Overhead shelter was assessed as the protection from rain provided by immediately overhanging wood and vegetation.

The approximate date on which incubation was started at a nest was calculated by backdating, using 18-20 days for incubation ($n=2$; pers. obs. and Best 1975), and nestling age. For nests found after hatching, nestling age was estimated (to $\pm$ 2 days accuracy) using developmental characteristics determined during this study from chicks of known age (Table 1).

Pairs were assumed not to be incubating or feeding young if the female and male fed quietly together, moved slowly, and swallowed all food gathered, for more than 15 min. Incubating females did not remain near the male, fed quickly, and rarely remained off the nest for more than 15 min. Males with incubating females gathered food to take to them.

DAYS	CHARACTERISTICS
1-2:	Chicks naked and blind; fluff on head; tarsus 8.5 mm (n = 2).
3-4:	Pterylae darkening; fluff on head; 0.5 mm frill along trailing edge of wings; tarsus 12.3 mm (n = 2).
5-6:	No feathers on pterylae; frill on wings 3 mm; eyes still closed; tarsus 15.5 mm (n = 2).
7-8:	Primary and contour feathers popping; sexes distinguishable; eyes opening; tarsus 19.7 mm (n = 2).
10-11:	Primaries unsheathed 5 mm; contour feathers covering most of body; tarsus 23.3 mm (n = 2).
> 11:	Body well feathered.

Table 1. Developmental characteristics of black tit chicks.

RESULTS

NESTING DENSITY

Thirty-seven nests were found in November 1987, of which 11 were located outside the main study area. The 9.6 ha study area contained 26 nests, giving a minimum breeding density of 2.7 pairs/ha. If black tits occurred at a similar density throughout the 180 ha of *Olearia/ Brachyglottis* forest and *Hebe elliptica* scrub on Main and Broughton Islands, Alert Stack and Daption Rocks, then the population of black tits was about 500 pairs. This estimate is conservative, as some pairs had territories solely within the 86 ha of tussock grassland, nesting in rock crevices around cliff edges (density of tits in tussock grassland was not estimated).

NEST SITE CHARACTERISTICS

Black tit nests (Fig. 2) were located in forest or on cliffs or exposed ridges. Two sites were known to have been used in more than one season (a ledge on an exposed rock used twice and a ledge inside a hut used four times). Thirty-four nests were in pure *Olearia* forest; an additional ten were in mixed *Olearia* and *Brachyglottis* or *Hebe* forest; one was in a pure stand of *Brachyglottis*, and four were on cliffs or exposed ridges. The canopy height and percent overhead cover in the vicinity of nests (Table 2) reflected typical forest height and density on the island. Ground vegetation in the vicinity of nest sites was a mix of ferns, *Callitriche* or *Crassula* swards, and *Poa* grasses.

Measurement	Mean	SD	*n*	Range
Canopy height (m)	4.4	1.4	46	4-7
Canopy cover (%)	53.2	25.6	45	10-100
Nest height (m)	0.64	0.57	49	0-3.5
Main entrance:				
width (cm)	14.5	7.4	40	4-30
height (cm)	13.8	7.1	40	3-40
Nest shelter (%)	88.3	14.1	49	50-100
Angle of view from nest (deg.)	29.5	36.5	49	0-180

Table 2. Characteristics of nest sites of black tits.

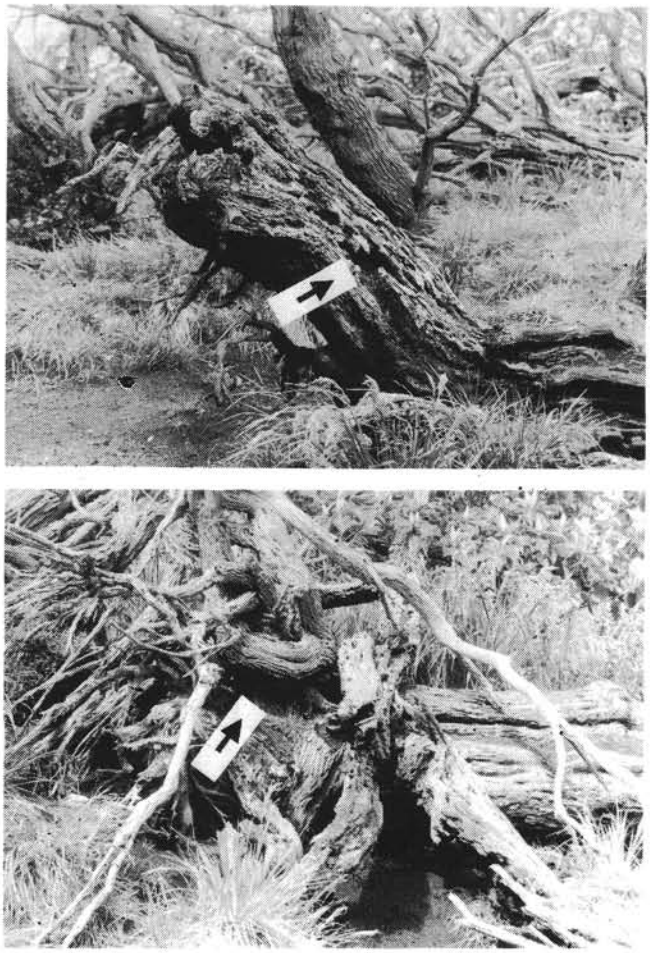

Figure 3. Sites of two black tit nests in *Olearia* trunks. Actual location of nests marked with arrow.

Thirty-eight nests were in stumps, trunks, or among roots of fallen logs of *Olearia* (Fig. 3); four were in trunks or roots of *Brachyglottis*; three were in *Polystichum vestitum* ferns; three were on ledges of banks or rocks, and one was under a *Poa astonii* tussock. Forty nests were within one metre of the ground, eight were between one and two metres, and one was 3.5 m above the ground. All nest sites examined were well drained, and all were well protected (usually by an overhanging shield of wood) from landing petrels. One nest in the bank of a creek would have been vulnerable to flooding; one on a coastal rock ledge was swept away by 5 m waves during a storm, although young had fledged from this site in 1985. All except one or two nests in ferns were built on a solid base. All but one were easily reached with a hand (the one exception was in a hollow log, with a 3 x 12 cm opening). Twelve nests had secondary entrances which were occasionally used by the birds; 24 had only one entrance less than 20 x 20 cm. The angle of view for an incubating female ranged from 0° to 180° and was not biased towards any compass direction. Most nests were well sheltered from rain.

CLUTCH SIZE AND NUMBER OF CHICKS

Clutch size for black tits was three (25 nests) or two (5 nests) (mean 2.83). At banding age (10-15 days after hatch), 13 nests contained three chicks, nine contained two chicks, and one contained one chick (mean 2.52). Most of the loss was due to infertile eggs. Only one nest was known to fail completely (destroyed by high seas - see above); however, fledging had occurred from only 17% of nests by the time we left the island.

TIMING OF BREEDING

Incubation began between 21 October and 2 December, with most laying in early November (Fig. 4). The late nest was under construction in mid-November, but the pair delayed laying for about two weeks. One territory-holding pair on the edge of the study area was not incubating or feeding young when we left the island.

Nine pairs were located during a visit to Southwest Promontory on 27 November. Of these, only three were incubating or rearing young (one with chicks, one on eggs, one not determined). Assuming that the other six pairs eventually bred, the mean laying date would have been much later than in the main study area.

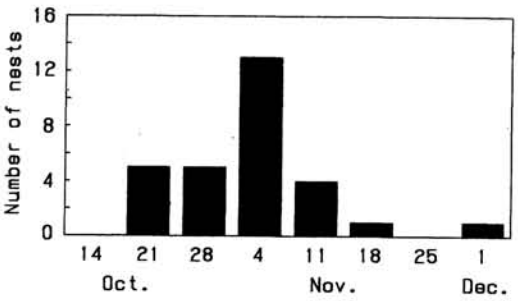

Figure 4. Week during which incubation started in black tit nests in main study area, Snares Islands, 1987. Date indicates beginning of week.

The first chicks to fledge in 1987 left their nest on 1 December, compared with 4 December in 1985 and 6 December in 1986. Later nesting was recorded in the 1982-83 season, when no fledglings were seen before 4 January and the chicks in one nest did not fledge until 20 January. Breeding of Snares Island snipe (*Coenocorypha aucklandica huegeli*) was also delayed in 1982-83 (Miskelly unpubl. data), possibly due to the El Niño event that summer (see Cane 1983, Barber & Chavez 1983, Schreiber & Schreiber 1984).

Black tit fledglings were fed by their parents for up to five weeks after leaving the nest, as one banded chick was still being fed by its father on 25 January 1987, 35 days after fledging. Thus a full breeding cycle for black tits (from start of nest construction to chick independence) may take 86 days (cf. 37 days for yellow-breasted tit; Kearton 1979). As laying is typically confined to the period from late October to early December (< 45 days), it is unlikely that black tits ever rear more than one brood in a breeding season. The latest nest recorded in 1983-84 held two large chicks on 7 January (Paul Sagar pers. comm.). Five adult black tits caught by Sagar between 6 & 13 January 1984 had all begun to moult primaries and contour feathers, and so were unlikely to breed again that season. Sagar's observations also suggest that black tits are single-brooded.

We have only one record of a pair of black tits renesting following a failed breeding attempt.

The female commenced incubating the original two egg clutch on 6 November 1985. One egg was lost by 10 November and the other egg was deserted. On 18 November the nest contained two new eggs (the egg from the first clutch was incorporated in the nest base) and a single chick fledged on 29 December 1985. Note, however, that only one of 37 pairs failed totally in its first breeding attempt in 1987.

DISCUSSION

Breeding densities of other subspecies of New Zealand tits have been estimated at 16 mainland locations and on 5 islands. Pied tit densities in stands of 4 different species of exotic conifers at Kaingaroa Forest ranged from 0.44 to 1.08 pairs/ha (data from Gibb 1961; breeding densities obtained by multiplying the total number of tits counted by the proportion of males recorded in October-November (0.92), and assumes that each male represented a breeding pair). Densities of pied tits on islands with one or more species of introduced mammalian predator ranged from less than 0.25 pairs/ha (Kapiti Island; Wilkinson & Wilkinson 1952, Kikkawa 1960) to 0.33-0.40 pairs/ha (Hen Island; Turbott 1940) and 0.39-0.63 pairs/ha (Little Barrier Island; Kikkawa 1964). Kikkawa (1966) reported densities of yellow-breasted tits at 14 South Island and Stewart Island locations ranging from 0.14 to 0.88 pairs/ha (mean 0.53 pairs/ha), and Kearton (1979) found a breeding density of 0.63 pairs/ha on Banks Peninsula. Densities of yellow-breasted tits on small islands ranged from 0.42 pairs/ha in the presence of rats (Ulva Island; Kikkawa 1966) to 5 pairs/ha on unmodified Little Solander Island (Miskelly unpubl. data, and see Cooper *et al.* 1986). The only tit population where density approached or exceeded the 2.7 pairs/ha found for black tits was on Little Solander Island. There are no figures available for the very dense population of Chatham Island tits on predator-free Rangitira (South East) Island (Miskelly, pers. obs.).

Dense populations of New Zealand tits have been found only on islands lacking mammalian predators (Snares Islands, Little Solander Island, Rangitira Island). In contrast, we found no correlation between tit densities at the 21 localities above, and the number of species or the biomass of small (< 30 g) insectivorous forest-dwelling passerines (likely competitors) present (Miskelly & McLean, unpubl. data). We suggest that it is the absence of predators, rather than the absence of competitors, that is the main factor contributing to high tit densities on some islands.

Nest sites for black tits were readily available in the tangled *Olearia* forest which dominates the Snares Islands. The main criteria for a site appeared to be that it provided a solid ledge for support, some protection from rain and large animals (particularly crash landing petrels), and could not be flooded. Fifty percent of nests had only one narrow entrance,which, when combined with their proximity to the ground and a limited view from the nest, would make incubating females subject to severe threat from any mammalian predator which established on the island.

Yellow-breasted tits on the South Island nest much higher off the ground than black tits. Kearton (1979) recorded heights for 16 nests in broadleaf/podocarp forest on Banks Peninsula as ranging from 1.75 to 8.0 m (mean, SD = 4.0 $\pm$ 1.9 m). This is significantly higher than nests on the Snares (t_{16} = 7.23, $P < 0.0001$). Yellow-breasted tits nesting in beech (*Nothofagus*) forest had even higher nests; 35 nests averaged 5.1 m from the ground (range 0 - 18.2 m; data from Ornithological Society of New Zealand (OSNZ) nest record scheme, analysed by Kearton 1979). Nest height is, of course, restricted by canopy height (rarely more than 5 m on the Snares), but the preference of black tits for hollow logs results in their nesting close to the ground.

The number of chicks fledged per breeding season by black tits was much lower than that reported for other tit populations (Table 3), due mainly to only one brood being raised per pair each breeding season (the mean clutch size was also smaller). Kearton (1979) gave a clutch size of 4.0 $\pm$ 0.9 eggs (range 3-6) in 15 pied tit nests, (data from OSNZ nest record scheme), and 4.1 $\pm$ 0.6 (n = 18 nests, range 3-6 eggs) for yellow-breasted tits. Clutch size of 24 Chatham Island tit nests on Rangitira Island in November-December 1983 was 3.3 $\pm$ 0.4 eggs (range 3-4 eggs, Miskelly unpubl. data). We note that evidence

Subspecies	Mean nesting density (pairs/ha)	Mean egg size (mm)	Clutch size Mean	Range	Incub'n period (days)	Nestling period (days)	Fledgling period (days)	No. of broods	Max. prod'n per pair
pied tit	0.54	17.7x15.3	4.0	3-5	16-17	17-18	c.21	up to 3	15
yellow-breasted tit	0.52	18.1x14.8	4.1	3-5	16	17-20	18-23	up to 3	15
Chatham Island tit			3.3	3-4	17-18	16-19		up to 2	8
black tit	2.7	20 x15.2	2.8	2-3	18-20	17-22	c.35	1	3
Auckland Island tit			3	3				up to 2	6

Table 3. Summary of the breeding systems of New Zealand tits. As no information was available on breeding success, we calculated maximum chick production per pair by multiplying maximum clutch size by the maximum number of broods raised per season. Sample sizes are not known for much of the data.
Sources: pied tit - Wilkinson & Wilkinson 1952, Oliver 1955, Gibb 1961; yellow breasted tit - Oliver 1955, Kearton 1979; Chatham Island tit - Miskelly unpubl. data; black tit - Oliver 1955, Best 1975, this study; Auckland Island tit - Fleming 1985.

for clutches of six is circumstantial, and no records of six chicks being fledged are available. Calculations in Table 3 use a five egg maximum.

Other tit subspecies have more protracted breeding seasons than black tits, allowing two or more broods to be reared. Wilkinson & Wilkinson (1952) gave the breeding season of pied tits on Kapiti Island as late August to February, during which two broods were reared. Gibb (1961) gave the laying season for pied tits in Kaingaroa Forest as late September to late December, with two or three broods being reared. Kearton (1979) recorded breeding (nest-building to chick independence) from 7 September to 24 February for yellow-breasted tits on Banks Peninsula, with up to three broods being raised per pair. Chatham Island tits on Rangitira Island laid between 16 October and 10 December, 1983, the latest nest being a second brood (Miskelly, unpubl. data).

The short breeding season of black tits on the Snares Islands is not an effect of living at a higher latitude, as Fleming (1985) reported that Auckland Island tits (at 50°40' S) laid from late September onwards and probably reared two broods.

As black tits raised fewer young each season, each chick had a greater proportion of the annual parental investment allotted to it. Actual parental investment per chick was also high, indicated by the large egg size, long incubation period, and long period of chick dependence (Table 3). The high parental investment in each black tit chick may increase the chick's ability to compete with conspecifics for territories and food, given the high density of tits on the Snares Islands.

Low per pair productivity has been found for other New Zealand passerines that occur at high densities on islands, viz fantail (*Rhipidura fuliginosa*) (Dennison *et al.* 1979, McLean 1984), New Zealand robin (*Petroica australis*; Flack 1976; also see King 1984), Chatham Island warbler (*Gerygone albofrontata*) (Dennison *et al.* 1984) and Bellbird (*Anthornis melanura*) (Sagar 1985). However, number of young raised by *Petroica* species may increase in response to a decrease in population density (Flack 1974), and black robins *P. traversi* respond to clutch removal by laying more eggs (Cemmick & Veitch 1985). Black tits at lower population densities (e.g. in the presence of a mammalian predator) could increase their productivity in response to decreased intraspecific competition, or lay further clutches after nests are destroyed. However, other constraints (low forest structure, the need for overhead protection from petrels) suggest that they could not build nests in less accessible places than they currently do.

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